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Citation style: Pawlik Łukasz, Buma Brian, Šamonil Pavel, Kvaček Jiří, Gałązka Anna, Kohout Petr, Malik Ireneusz. (2020). Impact of trees and forests on the Devonian landscape and weathering processes with implications to the global Earth's system properties – A critical review. “Earth-Science Reviews” (Vol. 205 (2020), Art. No. 103200), doi 10.1016/j.earscirev.2020.103200

Earth-Science Reviews 205 (2020) 103200

Contents lists available at ScienceDirect

Earth-Science Reviews

journal homepage: www.elsevier.com/locate/earscirev

Impact of trees and forests on the Devonian landscape and weathering processes with implications to the global Earth's system properties - A critical review

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ARTICLE INFO

Keywords:
Vascular plants
Trees
Silicate weathering
Biological weathering
Biogeomorphology
Climate change

ABSTRACT

Evolution of terrestrial plants, the first vascular plants, the first trees, and then whole forest ecosystems had far reaching consequences for Earth system dynamics. These innovations are considered important moments in the evolution of the atmosphere, biosphere, and oceans, even if the effects might have lagged by hundreds of thousands or millions of years. These fundamental changes in the Earth's history happened in the Paleozoic: from the Ordovician, the time of the first land plants, to the Carboniferous, dominated by forest ecosystems. The Devonian Plant Hypothesis (DPH) was the first concept to offer a full and logical explanation of the many environmental changes associated with the evolution of trees/forests that took place during this time period. The DPH highlighted the impact of deep-rooted vascular plants, particularly trees on weathering processes, pedogenesis, nutrient transport, CO_2 cycling, organic and inorganic carbon deposition, and suggests further possible consequences on the marine realm (oceanic anoxia and extinction during the Late Devonian). Here we attempt to combine the DPH and the related expansion in biodiversity, the Devonian Plant Explosion (DePE), with the Biogeomorphic Ecosystem Engineering (BEE) concept. This idea connects tree growth and activity with initiation and/or alteration of geomorphic processes, and therefore the creation or deterioration of geomorphic landforms. We focus on trees and forest ecosystems, as the assumed dominant driver of plant-initiated change. We find that whereas there is a broad evidence of trees as important biogeomorphic ecosystem engineers, addressing the DPH is difficult due to limited, difficult to interpret, or controversial data. However, we argue the concept of BEE does shed new light on DPH and suggest new data sources that should be able to answer our main question: were Devonian trees Biogeomorphic Ecosystem engineers?

1. Introduction

It is widely assumed that the Devonian Plant Explosion (DePE), i.e. the rapid diversification of plants on land, had far-reaching consequences on paleoclimate, paleopedogenesis, paleogeomorphology, and both terrestrial and marine environments. However, important biosphere/geosphere feedbacks are not fully explained to date, especially the relationship between plants, rock weathering and evolution of paleosoils. Science is still struggling to explain climate change and marine biota extinction (crisis) in the Devonian through empirical studies and modeling. Since we know the results (such as glaciation, formation of marine black shales related to anoxia), isolating the triggering factor (or factors) is challenging but interesting (Streel et al., 2000; Racki, 2005; Lu et al., 2019; Qie et al., 2019). To date, the global carbon cycle and changes in atmosphere carbon content are generally the main subject of speculation (Berner, 1992, 2006a, 2006b; Beerling and Berner, 2005; Royer, 2014).

Two main geomorphic processes are frequently mentioned in the context of climate change in the Devonian:

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https://doi.org/10.1016/j.earscirev.2020.103200
Received 30 January 2020; Received in revised form 24 April 2020
Available online 07 May 2020

1. silicate weathering, a process that consumes CO_2 (Kasting, 2019), with a substantial part of this carbon sequestrated in the oceans and buried as marine carbonates (e.g. Berner, 2006a; Eq. 1, p. 5653)
2. the accumulation of large amount of carbon by land plants during photosynthesis, forming rich coal deposits (Boyce and Lee, 2017).

It has been hypothesized that these two mechanisms resulted in a decrease of atmospheric CO_2, a subsequent drop in the greenhouse effect, and consequently continental glaciation in the Devonian and Permo/Carboniferous era (Streel et al., 2000; McGhee, 2005; Royer, 2014; Goddéris et al., 2017). Another hypothesized effect was the Devonian Marine Crisis (DMC), one of the most significant marine extinctions in the Paleozoic. Some authors have argued that deep-rooted vascular plants contributed to weathering and soil production, and the resultant material (such as nutrients released from silicate and phosphate weathering), when transferred to ocean basins, caused marine anoxia and extinction (Algeo et al., 1995; Algeo and Scheckler, 1998; Algeo et al., 2001; Morris et al., 2015; Qie et al., 2019). Wildfires and subsequent soil erosion could be source of erosional materials to the ocean as well, as atmospheric oxygen levels increased over 17% in the Late Devonian (Glasspool et al., 2015; Rimmer et al., 2015). This suggests a positive feedback between higher proportion of P available in the soils (stimulating plant growth; P is an essential and often limiting nutrient), and the plants would then enhance weathering processes (Morris et al., 2015).

Here, we explore the role and significance of the evolution of trees in the DePE as it relates to global climate at that time and the DMC. Trees are a powerful driver of geomorphic change, and we explore their effectiveness as Biogeomorphic Ecosystem Engineers (BEEs) in the Devonian, the period when vascular plants, trees and forests first emerged (Kenrick and Crane, 1997; Scheckler, 2001; Lu et al., 2019). In particular, we are interested in the implications of the DePE on ancient landforms and weathering processes, with an eye towards the role of the tree growth forms emergence on climate change and/or subsequent mass extinction.

This complex issue of trees and soil/regolith/bedrock interactions has been explored several times but in different scientific contexts, such as dynamic pedogenesis, biological energy in landscape evolution, terrestrialization in the Devonian, silicate weathering, and climate change (Algeo et al., 1995; Johnson, 2002; Phillips, 2009a; Goudie and Viles, 2012; Mitchell et al., 2016). We hypothesize that the evolution of trees and especially fungal-associated (mycorrhizal) tree roots (at least partially) drove Devonian climate change via new geomorphic weathering processes.

We must first describe the concept of the Devonian Plant Hypothesis (DPH) (Algeo et al., 1995).

The DPH is an attempt to explain climate changes and mass extinctions that occurred during the Late Devonian period (Kellwasser crisis at FF, Frasnian/Famennian, boundary and Hangenberg crisis at Devonian/Carboniferous transition), one of the most dramatic losses of diversity in the planet's history (Racki, 2005). The DPH, initially proposed by Algeo et al. (1995) as the Devonian plant-weathering hypothesis, connects the extensive black shales and other minerals which indicate low oxygen availability with the expansion of plants (and especially forests) across terrestrial surfaces at that time. The increase in plant material likely contributed to eutrophication in shallow seas and drove increased silicate weathering, reducing CO_2 globally (following this chemical reaction: $[CO_2 + (Ca, Mg)SiO_3 \rightarrow (Ca, Mg)CO_3 + SiO_2]$, during which CO_2 is derived from the atmosphere) and reducing global temperatures, which potentially caused short but intense periods of glaciation (Beerling, 2002; Berner, 2006a, 2006b; Isaacson et al., 2008; Algeo and Scheckler, 2012; Kasting, 2019; Wan et al., 2019).

Although the broad role of plants in the DPH is well established, recent advances in the study of BEE, and in particular the role of roots in bedrock weathering and soil production, may refine this hypothesis (Fig. 1). Here, we wish to apply new understandings of these complex interactions to the Devonian, the period of probable biologically driven weathering revolution, explosion in plant diversity, and the evolution of the Earth's first forest ecosystems (Algeo et al., 2001; Berner, 2001; Kenrick and Davis, 2004; Lu et al., 2019). In particular, we want to discuss the DPH in the light of recent discoveries in the concept of ecosystem engineering (Jones et al., 1994, 1997), biogeomorphology (Coombes, 2016; Viles, 2019), and eco-evolution theory (Corenblit et al., 2011). Modern trees frequently act as BEEs, highly modifying their geomorphic and lithic environment. But did early trees?

Taking into account Devonian landforms (even if largely speculative), ecosystems and information on the early evolution of plants we try to answer the question whether Devonian trees were capable of increasing weathering rates of terrestrial rocks similar to modern rates. While discussing geomorphic role of trees we also point to the counter hypothesis, that BEEs were not significant, by outlining the most important abiotic forces which might have caused climatic fluctuations in the Devonian in contrary or in connection to biotic forcing of the Paleozoic climate (Section 2).

2. Devonian plant explosion, the impact of trees and first forest ecosystems in the Earth history

Land plants likely arose during the Early-Middle Ordovician (478-458 Ma), or slightly earlier (via molecular inferences, Morris et al., 2018), from charophycean green algae (Graham, 1993; Kenrick and Crane, 1997; Willis and McElwain, 2002; Wellman, 2004; Salamon et al., 2018; Servais et al., 2019). Vascular plants appear later, after another 20-50 million years. The first known example is the small and very simple vascular plant *Cooksonia* (Lang, 1937; Edwards et al., 1992) of which the oldest fossils were found in the Czech Republic (ca 432 Ma; Libertín et al., 2018a, 2018b). Fungi, which can also impact mineral weathering (Quirk et al., 2012, 2015; see also Section 6) probably developed much earlier, 900 million years ago (Heckman et al., 2001; Taylor et al., 2015; Loron et al., 2019). They likely aided in the establishment and radiation of land plants (Pirozynski and Malloch, 1975; Simon et al., 1993; Brundrett, 2002; Berbee and Taylor, 2007; Bonfante and Genre, 2008; Smith and Read, 2008; Field et al., 2012; Morris et al., 2015). Thus from the beginning land plants and fungi likely collaborated (Remy et al., 1994; Taylor et al., 1995, 2015; Taylor et al., 2009; Gensel et al., 2001; Hoffland et al., 2004; Field et al., 2015; Selosse et al., 2015). This symbiosis has been tested and illustrated through analysis of the fossil plant record from the 407 million yr-old Rhynie Chert (Strullu-Derrien et al., 2014), and seems a relatively solid.

Trees play an outsized role in shaping the surface of the land, as they are the interface for a variety of complex interactions and strong feedbacks between Earth's biotic and abiotic components (e.g. Amundson et al., 2007). For example, absorption of atmospheric carbon dioxide via photosynthesis and fixation into long lived biotic compounds (e.g., lignin), plus root-driven enhanced silicate weathering and subsequent CO_2 declines, likely resulted in significant cooling of the Earth's climate (Berner, 1998, 2001; Beerling and Berner, 2005; Le Hir et al., 2014; Royer, 2014). It should be noted that alternative hypotheses do exist that often stress purely abiotic climate forcings, e.g. arc-continent collisions and orogeny (Goddéris et al., 2017; Macdonald et al., 2019), continent spatial configuration against the equator (Scotese, 2016; Scotese and Wright, 2018; Fig. 2), or large igneous eruptions (Racki et al., 2018; Racki, 2019) (Table 1). It is also argued that the inorganic carbon cycle (carbonate-silicate cycle) is more important than the organic carbon cycle in controlling atmospheric CO_2. However, in general, the contribution of living organisms to the Earth surface dynamics has been widely acknowledged during the past decades (Schwartzman and Volk, 1989; Phillips, 2009a; Sullivan et al., 2016; Viles, 2019; Porder, 2019).

Of relevance to climate and plant-landform interactions is the ways in which trees limit, promote, and interact with regolith and bedrock. Weathering processes, and especially biological weathering, are

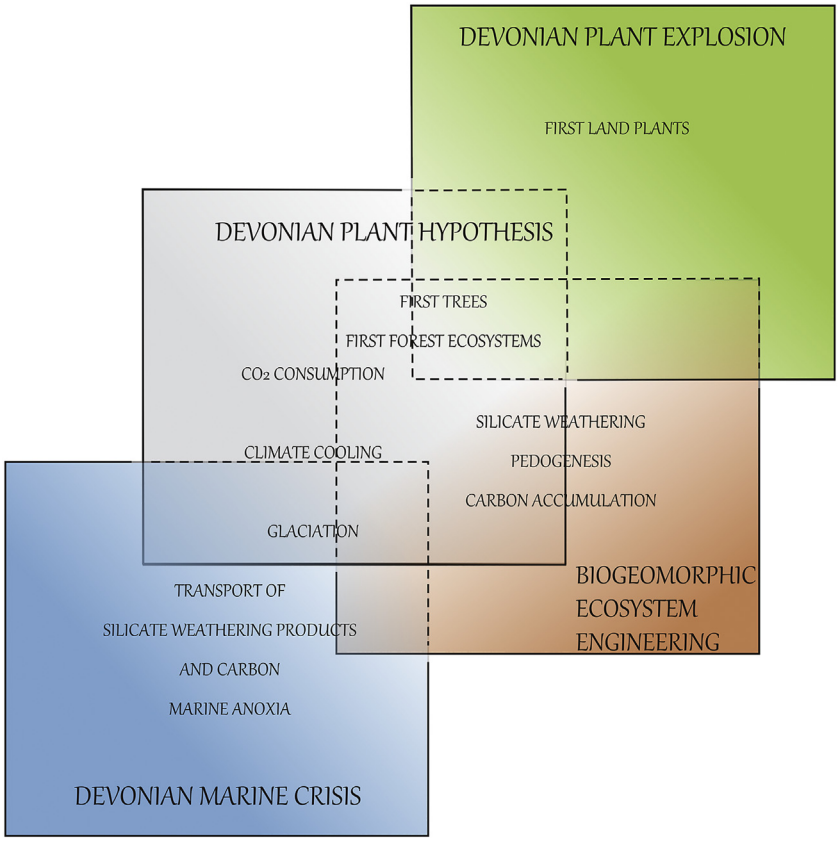

Fig. 1. Relationship between four concepts considered in the present study. DePE and DMC are geological facts proved by empirical data. DPH and BEE are concepts which can help to define a direct link between those two fundamental events. Authors' unpublished figure.

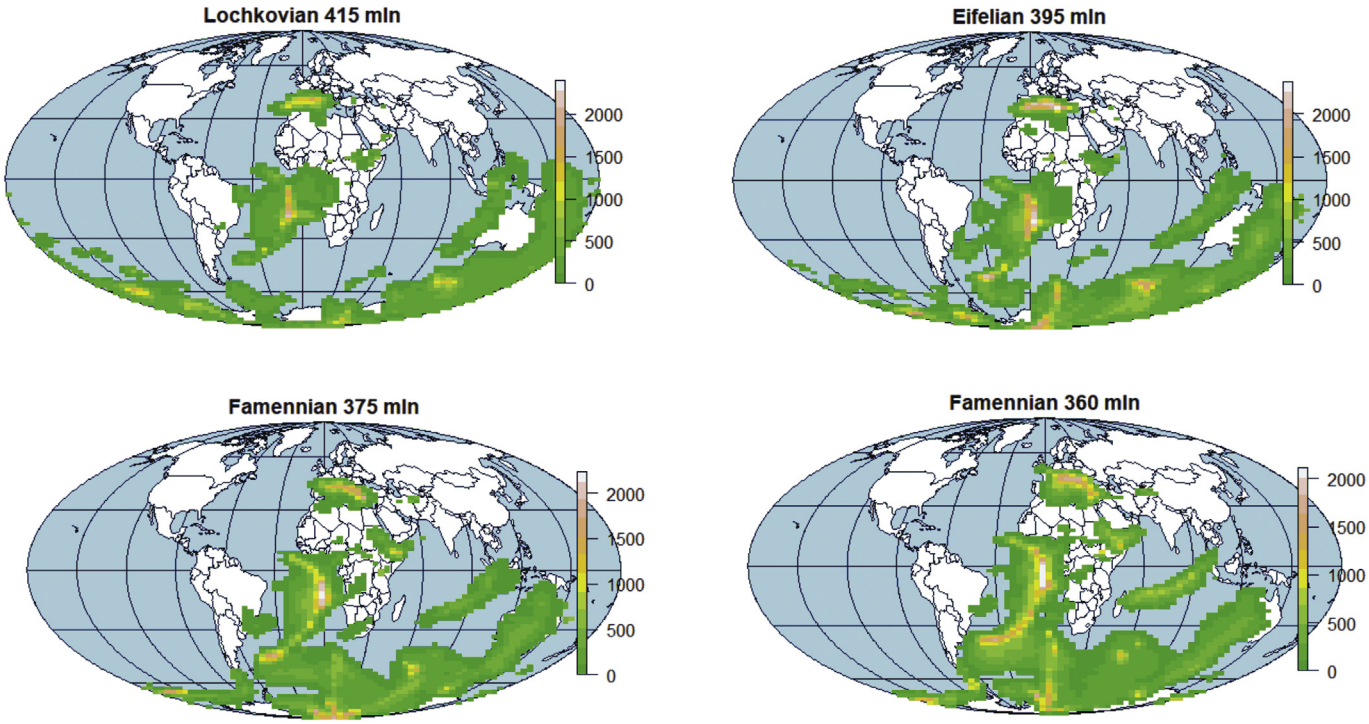

Fig. 2. Spatial configuration of continents in the Devonian superimposed on their current configuration. Data source: www.earthbyte.org/paleodem-resource-scotese-and-wright-2018/. The figure displays raster model for land only, thus no elevation scale is shown.

Table 1
Climatic trends in the Phanerozoic forced by global tectonics and plant evolution.

Triggering factor	Direct effect	Climate response	Reference
1. Latitudinal position of the continents	1. Increase in CO_2 consumption by silicate weathering when continents were in low latitude position	1. Climate cooling	1. Goddéris et al., 2014
2. Land mass homogeneity - supercontinents vs. small continents	2. Arid conditions associated with supercontinents weaken silicate weathering thus promoting high levels of pCO_2	2. Climate warming	2. Macdonald et al., 2019
3. Arc-continent collisions in the tropics and orogeny	3. Increase global weatherability, CO_2 decline	3. Climate cooling	3. Macdonald et al., 2019
4. Tectonics and mountain uplift	4. Regolith removal by erosion and increase in chemical weathering	4. Climate cooling	4. Goddéris et al., 2017
5. Evolution of land plants	5. Global modification of albedo, temperature, precipitation, and air circulation (the influence of surface roughness)	5. Climate cooling	5. Boyce and Lee, 2017

frequently difficult to detect or study but are pervasive and significant over long timespans (Phillips et al., 2019; Anderson, 2019). Weathering processes are key to long-term landscape evolution theories and models. Although biological weathering has been studied to some extent for decades, a number of key aspects of this fundamental process still require a satisfactory explanation (e.g., Yatsu, 1988; Anderson, 2019), and the role of trees in weathering processes awaits full recognition (Pawlik et al., 2016a). For instance, plants devoid of microorganisms do not exist under natural conditions so separation of individual effects of plants and microorganisms is still a problem (R. Finlay et al., 2019a; R. D. Finlay et al., 2019b). Similarly, it is frequently assumed that trees break up bedrock thus contribute to soil production via their root system. Kenrick and Davis (2004) wrote in their popular „Fossil Plants" book that "…*[roots] can break up rock, bind loose particles together, and they provide a conduit for the movement of water and solutes, all of which are essential to the development of soils*" (p. 47-48). However, the whole story is related not only to root properties *per se* but also to bedrock type/structure, and mutual interactions between roots and soil biome within rhizosphere and mycorrhizosphere. Thus, in the light of the two concepts which are the focus of this paper, DPH and BEE, and in particular the role of trees and forests, the most fundamental question is what role tree roots play in biological weathering and initial soil production, only recently tested empirically (Malik et al., 2019).

The first identified tree-form plant is *Wattieza*. Although *Wattieza* assumed a tree habit early (Stein et al., 2007), with an extended trunk and considerable height, its root system appears to have been quite small and dense, likely contributing to the stability of the surface soil (Meyer-Berthaud et al., 2010), but limiting its impact on deep weathering. Extensive and deep root systems, more similar to many modern trees, are not found until *Archaeopteris* in the early Givetian 388-383 Ma (Banks, 1970; Thomas and Spicer, 1987; Guo and Wang, 2011; Stein et al., 2019). Extensive roots likely evolved several independent times after this (Kenrick and Strullu-Derrien, 2014). Owing to their great abundance, Beck (1981) argued that *Archaeopteris* might have been able to form extensive forest ecosystems itself, influencing the ecology of late Devonian plant communities and Devonian landscapes. This, along with their other properties such as 20 m height trunks and 1.6 m deep root systems (Table 2), suggests *Archaeopteris* probably played a weathering role similar to present trees (McGhee, 2018; Stein et al., 2019).

However, full landscape occupation by forest ecosystems has been recently questioned by Boyce and Lee (2017) who noticed that the early record of vascular plants is dominated by wet lowland environments (Table 3; see also Lu et al., 2019), and the true first evidence of upland plant colonization comes from the earliest Carboniferous (Bateman and Rothwell, 1990). In fact, this discussion dates back at least to Barrell's (1913) view that Late Devonian forests formed streamside galleries and dry interfluves were colonized by herbaceous or bushy vegetation (Retallack, 1985). Falcon-Lang (2005) also speculates that before 360 million years ago (before the evolution of tree seed habit), the Earth's mountains were probably bare of vegetation. Different Ordovician and Silurian landscapes are presented in their review by Edwards et al. (2015) where they focus on cryptogamic covers (CCs), which may also be significant via chemical weathering. Based on their experimental results, Quirk et al. (2015) suggested limited liverwort-driven weathering, owing to their shallow rhizoids. But recently Porada et al. (2016) suggested a high potential for chemical weathering of non-vascular plants in the Late Ordovician. Regardless, by the early Silurian Morris et al. (2018) argue that plants developed key adaptations for survival and proliferation on dry lands (e.g. cuticle, stomata, sporopollenin) and for effective soil-plant interactions (rhizoids, rhizomes, symbiosis with mycorrhizal fungal partners).

In sum, it is unclear whether early trees were limited in their spatial extent or if there is just a lack of proper evidence supporting the hypothesis of widespread distribution of Devonian trees (Fig. 3). The DPH assumes this spatial limitation which was only eliminated with the development of tree seed habit (Algeo et al., 2001). Before 360 million years ago early trees used pteridophytic (fern-like) reproductive mode, limiting their survival and dispersal substantially. Meyer-Berthaud et al. (2010) speculates that pseudosporochnalean trees probably inhabited places with no water limitation during the growth season, due to constraints imposed by their small root systems and large amount of living cells forming the trunk. Falcon-Lang (2005) also argues that a consequence of seed evolution in the Late Devonian (360 Ma) was plants were capable of growing in dry upland environments. Indeed, Schumm (1968) assumed that vegetation cover was limited to nearshore and coastal-plain areas till the end of the Paleozoic Era. He developed his idea based on variety of hydrologic data and geomorphic observations. Even if forests were limited to the sides of streams, trees would then be able to change Devonian landscapes by forcing the evolution of meandering and anastomosing rivers (Schumm, 1968; Gibling and Davies, 2012). During this key period in the Earth history *"River systems co-evolved with plants and animals, generating new ecospace that we infer would have promoted biological evolution."* (Gibling et al., 2014) (Fig. 4). Floodplain forests were well developed by the Late Devonian, but the timeline of hillslope stabilization and tree-catalyzed weathering remains unanswered. The main constraint is the lack of evidence. Root traces occurring in oxidized paleosols of the Cap-aux-Os Member (Emsian, Gaspé, Canada) suggest occupation of more xeric (dry) sites and might be the only known example of the early land plants expansion towards drier uplands (Hotton et al., 2001). Overall it is clear that trees influenced floodplain evolution and geomorphology, but the timeline of hillslope colonization remains open, with clues that it occurred early inferred from other processes but little solid physical evidence of early colonization to date.

3. Biogeomorphic Ecosystem Engineering (BEE)

Some organisms can directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. This ability has called "ecosystem engineering" (EE) or physical ecosystem engineering (Jones et al., 1994, 1997; Gutiérrez and Jones, 2006). So far, two types of organisms have been proposed: autogenic physical engineers (AuPE; or endogenous engineers) and allogenic physical engineers (AlPE; or exogenous engineers).

Table 2
Main properties of first trees and forests. Some data is missing, marked as '-'.

Fossil taxon	Age	Root depth	Tree height	Reference
Calamophyton (Cladoxylopsida)	Mid Eifelian – Mid Givetian (393-382 Ma)	-	-	Giesen and Berry (2013)
Xinicaulis lignescens (Cladoxylopsida)	Early Late Devonian (Frasnian, ca. 374 Ma)	-	-	Xu et al. (2017)
Eospermatopteris/Wattieza (Cladoxylopsida)	Gilboa forest, NY, at least 385 Ma	-	8-12.2 m (26.2 -40 ft)	Banks (1970); Stein et al. (2007)
Pseudosporochnales (Cladoxylopsida)		*Duisbergia* - 0.3 m	8-12 m (26.2-39.4 ft)	Stein et al. (2007); Giesen and Berry (2013)
Protolepidodendropsis (Lycophytes)	Svalbard lycopsid forest (Late Devonian; Frasnian, 383-372 Ma)	-	At least 1.3 m (4.3 ft)	Berry and Marshall (2015)
Lepidosigillaria (Lycopodiopsida)	Middle Devonian	-	At least 4.9 m (16 ft)	Banks (1970)
Guangdedendron (Lycopodiopsida)	Upper Devonian (Famennian, 372-359 Ma)	-	1.1-7.7 m (3.6-25.3 ft)	Wang et al. (2019)
Lepidodendron (Lycopodiopsida)	Frasnian (383-372 Ma)	> 1 m (> 3.3 ft) (12 m (39.4 ft) in length!)	10-35 m (32.8-114.8 ft)	Willis and McElwain (2002)
Archaeopteridales (*Archaeopteris*) (Progymnospermopsida)	Earliest forests (Catskill are, NY, at least 385 Ma)	1.0 m (3.3 ft)	8.5 – 20 m (28 – 65 ft)	Goldring (1924); Beck (1981); Driese et al. (1997); Kenrick and Davis (2004)
	Cairo forest, NY, mid Givetian (385 Ma)	1.6 m (5.3 ft) and 10 m (32.8 ft) in length	-	Stein et al. (2019)
Forest at Trout Run, Pennsylvania	Upper Devonian (Famennian, 372-359 Ma)	Taproots extending to the depth of 1-1.5 m (3.3-4.9 ft)	-	Driese et al. (1997)

AuPE transform the environment directly via endogenous processes (e.g. tree growth) that alter the structure of the engineer, and the engineer remains as part of the engineered environment (Jones et al., 1997). AlPE change the environment by transforming living or non-living materials from one physical state to another, and the engineer is not necessarily part of the permanent physical ecosystem structure (e.g. beavers) (Jones et al., 1997). The concept of ecosystem engineering is broadly related to ecological niche construction (NC) and keystone species (KS). Niche construction theory assumes that environmental changes caused by organisms can lead to modification of selection pressures and to subsequent changes in the evolutionary trajectories of natural populations (Matthews et al., 2014). Recently, biogeomorphology and eco-evolutionary dynamics adopted these concepts and emphasized significant feedbacks between biotic and abiotic component of the terrestrial ecosystems on different spatial level of landscape complexity (Pelletier et al., 2009; Corenblit et al., 2011; Hendry, 2019).

An AuPE species can be a niche constructor because the physical changes influence chemical fluxes and species interactions can be large, multidimensional, and persistent (Matthews et al., 2014). One example can be found in tree uprooting. Soil movement and mixture due to tree tipping changes pedogenic processes (e.g. Šamonil et al., 2018a, 2018b; Pawlik et al., 2019) and microclimate (e.g. Schaetzl, 1990; Kabrick et al., 1997) on the resultant pits and mounds in the soil, which significantly influences ability of trees to regenerate on these microhabitats (Simon et al., 2011; Šebková et al., 2012; Pawlik et al., 2013; Šamonil et al., 2016). An ecosystem engineer can also be a keystone species, whose top-down effect on species diversity and competition is large relative to its biomass dominance (definition after Davic, 2003). All three concepts (autogenic physical engineering, niche construction, and ecosystem engineering) can be applied to modern trees. The remaining question is whether the Devonian trees played similar roles?

We hypothesize, following the initial assumption of Jones et al. (1994, 1997), that AuPE processes are significant in geoecosystems and operates across a range of scales and timeframes (Corenblit et al., 2007; Corenblit and Steiger, 2009; Corenblit et al., 2011; Jones, 2012; Eichel et al., 2016). In terms of trees and forest ecosystems the ecosystem engineering concept was frequently adopted to explain their substantial environmental impact (e.g. Phillips et al., 2017). However, their influence on weathering processes, and especially weathering processes in the Devonian, still awaits full exploration. Jonathan D. Phillips proposed biogeomorphic ecosystem engineering (BEE) concept and illustrated their effectiveness in karst landscapes (Phillips, 2016a, 2018) and forested hillslopes (Phillips et al., 2017). This term is similar to 'biogeomorphic engineering' (Francis et al., 2009) for erosion and accumulation processes induced by vegetation communities in fluvial systems. The ecosystem engineering is considered biogeomorphic when it involves biotic effects on landforms and geomorphic processes (Phillips, 2016a). The concept built primarily on Jones et al. (1994, 1997) works but also the idea of extended phenotype (Dawkins, 1982, 2004; Mitton, 2003) applied then to soils and landforms (Phillips, 2009b, 2016b). The extended phenotype refers to all environmental effects of a gene through an organism's activity and, in terms of soils, reflects the genetic evolution of traits on soil morphology (Phillips, 2009b). The synergistic effect of these new evolved features (e.g. deep

Table 3
Environmental conditions and geomorphic configuration of the earliest forest ecosystems.

Name	Site description	Reference
Xinhang lycopsid forest	Coastal environment, probably under the influence of saline water, similar to modern mangroves	Wang et al. (2019)
Gilboa forest	Coastal clastic swamp (waterlogged conditions as suggested by limited depth of roots) subject to periodic flooding, tropical-subtropical climate	Stein et al. (2007, 2012)
Cairo forest	distal floodplain system in a subtropical to temperate wetland environment (well-drained soils with periodic wet/dry seasonality)	Stein et al. (2019)
Forest of archaeopteridale (Archaeopteris)	„Upland" alluvial environment (moist, well-drained, and oxygenated soil conditions	Driese et al. (1997); Mintz et al. (2010)
Svalbard forest	Wet soils in rapidly subsiding, short-lived basin	Berry and Marshall (2015)
Arborescent Lycophytes (Lepidocarpales)	Swamps (shallow rooting system)	Thomas and Spicer (1987)

Fig. 3. Landscape reconstruction near to Prague, Czech Republic showing aluvial plain in small river delta with stands of *Pseudosporochnus*, up to 4 m high, with *Protopteridium* in shruby layer and herbaceous *Drepanophycus* and *Protolepidodendron* in understorey (Author: Jan Sovák, reprinted with permission of the Author).

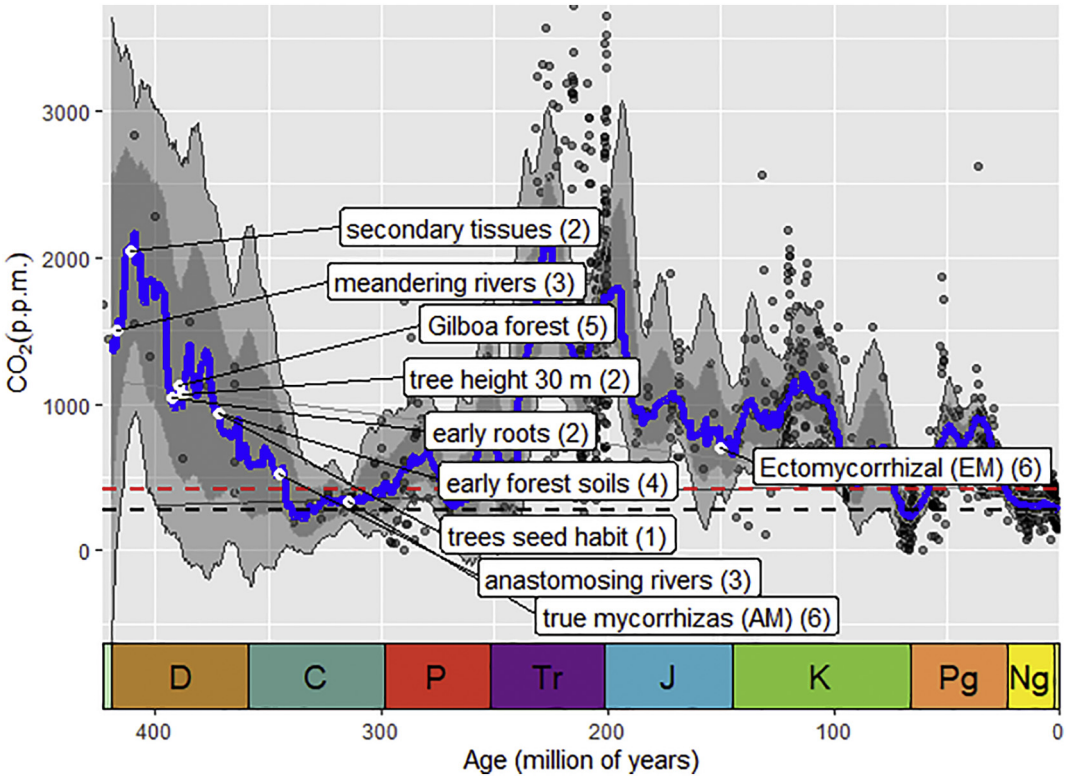

Fig. 4. Selected evolutionary stages against reconstructed atmospheric CO_2 content proxy data. We used data from Foster et al. (2017). A blue line is the most likely LOESS fit through the data. A dark gray band is 68%, and light gray band is 95% confidence interval. Horizontal bars at x-axis indicate eras, starting from Silurian (S) to Neogene (Ng). The geological scale is after Cohen et al. (2013) and a *deeptime* R package (Gearty, 2020). The dark dashed line indicates the lowest calculated atmospheric CO_2 content. The red dashed line indicates the current level of atmospheric CO_2. References used for this figure listed alphabetically: (1) Algeo et al. (1995); (2) Algeo and Scheckler (1998); (3) Gibling and Davies (2012); (4) Retallack (2001); (5) Stein et al. (2007); (6) Strullu-Derrien et al. (2018).

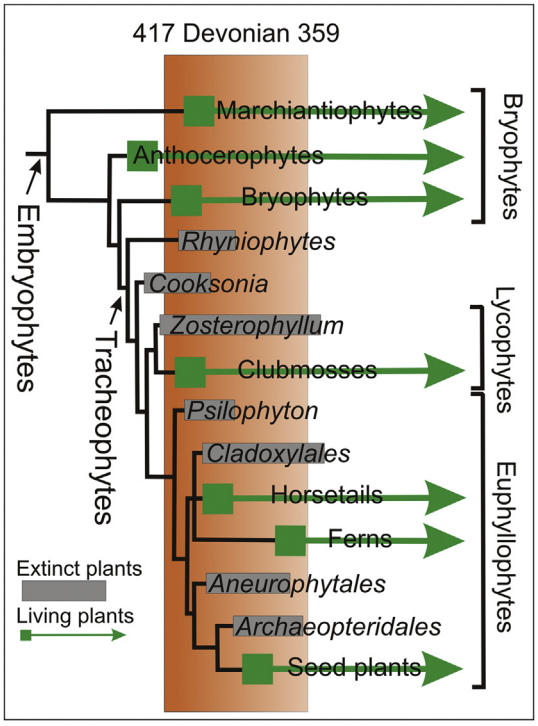

Fig. 5. Simplified phylogenetic tree of the early land planst and their origin and diversification in the Devonian. Autohrs unpublished figure based on Strullu-Derrien et al. (2014). Embryophytes – land plants, Tracheophytes – vascular plants, bryophytes – non-vascular plants (liverworts, hornworts and mosses), Lycophytes – spore-bearing vascular plant, Euphyllophytes – vascular plants with 'true' leaves.

root systems, arborescence) might be considered under the BEE concept, thus extending argumentation supporting the DPH. Clearly land plants led to evolution of new pedotypes (Retallack, 2001) and changed the character of fluvial systems from braided to meandering in the Devonian (Gibling et al., 2014). Anastomosing river systems probably developed in the Missisipian, ca. 345 million years ago (Gibling et al., 2014). As such it is reasonable to assume some biogeomorphic effects directly resulting from the evolution of trees.

Probably the most important innovation that help land plants and especially trees to become biogeomorphic ecosystem engineers were roots. Roots developed from 419 to 408 million years ago and immediately developed physiological mechanisms to regulate their growth (gravitropism, polar auxin transport regulation) (Kenrick and Strullu-Derrien, 2014; Xue et al., 2016). This happened at least twice: during radiation of Lycophytes (fern-like plants) and Euphyllophytes (Strullu-Derrien et al., 2018) (Fig. 5). Although the first tree roots were very small, 1-2 cm in width (resembling roots of some modern palms), they were able to contribute to ground stability because of fast establishment of trees (Kenrick and Strullu-Derrien, 2014). Before the time of 'true roots' development, soil stabilization had been partly achieved by rhizomes of lycopsid *Drepanophycus* (Xue et al., 2016) and others. Prior to true rooting development, potential weathering effects were likely minor but represent a transition moment from limited ecosystem engineering (due to 1. low number of engineering organisms, 2. their limited spatial redistribution, and 3. the lack of, or small, rooting systems) to biogeomorphic dominance of BEEs (Phillips et al., 2017) triggered by the expansion of forest ecosystems in the Lower Devonian (though, as noted above, there is still uncertainty regarding the spatial extent of this early forests - a global scale or limited to wet lowland areas, e.g. coastline forests, lowland floodplain forests, and swamps) (Fig. 6). Before the evolution of trees, other land plants developed quite deep root systems as those reported by Elick et al. (1998) from Gaspé Bay, Québec (Canada). Emsian (407-393 Ma) in age, these plant roots were 0.5-2 cm thick and 10-90 cm deep. It appears the engineering effects of these non-tree plants and their roots would have been limited to plant anchoring and ground stabilization (as opposed to facilitating weathering), because they grew in highly-energetic conditions of ephemeral alluvial plain controlled by frequent avulsion events. Additionally, no traces of chemical or pedogenic alteration of bedrock have been found around roots (Elick et al., 1998).

4. Tree roots, their symbiotic microorganisms and the way they drive weathering processes

The hidden world of bedrock weathered by tree roots and associated microorganisms (especially bacteria and fungi) or their symbiotic counterparts (mycorrhizae) has long been a subject of speculation (since at least Gilbert, 1877, and Shaler, 1892; see a review by Pawlik et al., 2016a). The initial statement formulated by Gilbert (1877), that plant roots can *"pry apart rocks"* was partly demonstrated some 70 years later (Jackson and Sheldon, 1949) but seriously criticized by Yatsu (1988) in his famous book "*The Nature of Weathering: an introduction*". However, appreciation of this aspect of biological weathering has been significantly improved through studies on microbial geomorphology (Viles, 2012), regolith formation (Hasenmueller et al., 2017), bacterial and fungal communities (Uroz et al., 2009), mycorrhizae (Bornyasz et al., 2005; Gadd, 2007), and tree root morphology and wood anatomy (Malik et al., 2019).

Special attention to trees is reasonable because it is assumed that they have greater influence on weathering processes than other plants due to their size, longevity, and depth of root zone (Miles, 1986; Binkley and Giardina, 1998; Pawlik, 2013; Pawlik et al., 2016a, 2016b). Mycorrhizae, which facilitate symbiotic interactions between host plant and fungi, are common and exist in over 90% of natural land plants (Brundrett and Tedersoo, 2018). Mycorrhizal association with arbuscular mycorrhizal fungi (AMF) is among the most ancient symbiosis, and evolved in early land plants (Field et al., 2015). AMF form symbioses with 72% of vascular plants (Brundrett and Tedersoo, 2018), and are generally fully dependent on host plants for carbon as they typically lack saprotrophic capabilities (Smith and Read, 2008). Up to 30% of photosynthetically assimilated carbon is directly transported by host plant to mycorrhizal fungi or released from roots (Leake et al., 2004). In exchange, AMF provide a broad spectrum of beneficial functions to their host plants as well as to their environments like improved nutrient and water uptake, enhanced tolerance against biotic and abiotic stresses and improved soil structure to counteract soil erosion.

Endomycorrhizal fungi penetrate plant root tissue in both intercellular space and inside cells. Colonization of the root interior by endomycorrhizal fungal hyphae causes both morphological and physiological changes in both symbionts, e.g. changes in the composition and amount of root secretions and glomalin production (Gałązka and Gawryjołek, 2015; Gałązka et al., 2017, 2018). Many AMF have been classified in the phylum *Glomeromycota*. Production of glomalins is primarily carried out by fungi from the genus *Glomus*. In the other representatives of the phylum *Glomeromycota*, the ability to produce glomalins has not been detected, except for the small amounts of glomalins produced by the genera *Gigaspora* and *Acaulospora* (Blaudez et al., 2000). It was *Glomeromycota* that was already found in the early Devonian (Dotzler et al., 2006). These fungi were undoubtedly of decisive importance in the development of Devonian plants.

Spores of *Glomeromycota* from the Lower Devonian provide the first evidence for germination shields in fossil fungi and demonstrate that this complex mode of germination was in place in some fungi at least 400 million years ago (Strullu-Derrien et al., 2018). Moreover, they represent the first direct marker relative to the precise systematic position of the Early Devonian endomycorrhizal fungus (*Glomeromycota: Diversisporales, Gigasporaceae*). These structures are regarded as a derived feature within the phylum *Glomeromycota*, and hence their

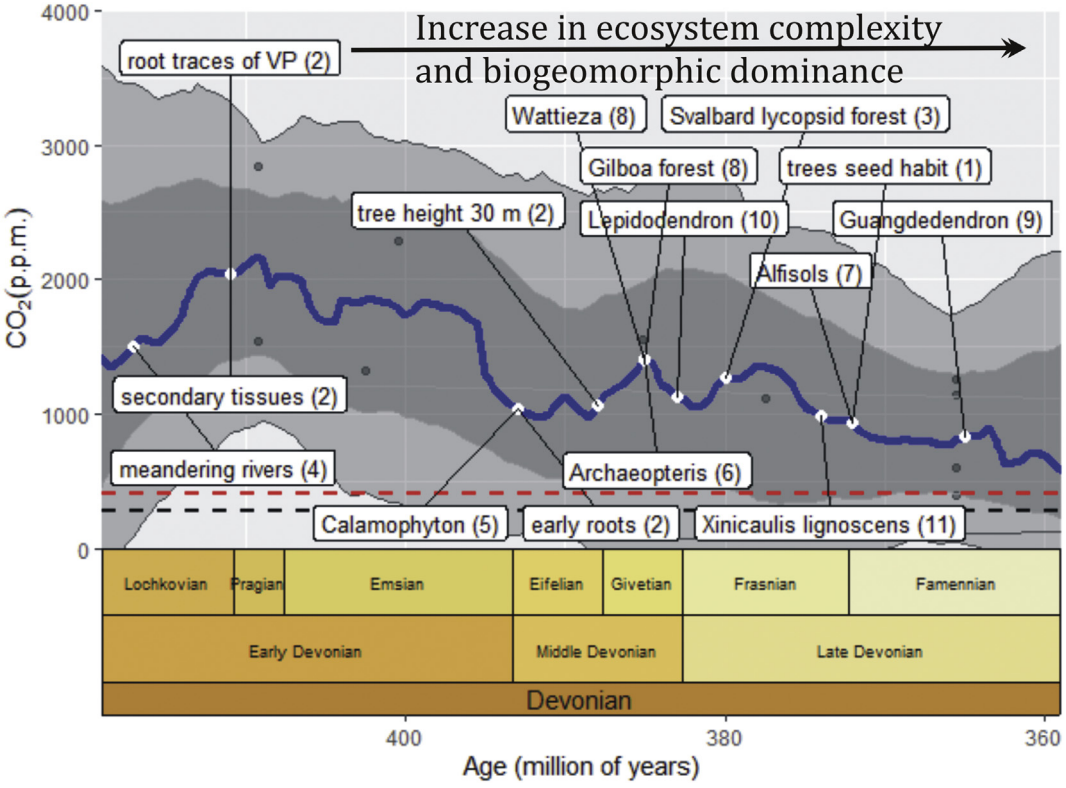

Fig. 6. A close look at trees diversification and selected accompanying events in the Devonian. Authors' unpublished figure. The geologic time scale after Cohen et al. (2013) and applied in a *deeptime* R package (Gearty, 2020). Atmospheric CO_2 content data after (Foster et al., 2017). See also Fig. 4 caption for description. References used for this figure listed alphabetically: (1) Algeo et al. (1995); (2) Algeo and Scheckler (1998); (3) Berry and Marshall (2015); (4) Gibling and Davies (2012); (5) Giesen and Berry (2013); (6) Goldring (1924); (7) Retallack (2001); (8) Stein et al. (2007); (9) Wang et al. (2019); (10) Willis and McElwain (2002); (11) Xu et al. (2017).

presence in the Rhynie chert suggests that major diversification within this group of fungi occurred before the Early Devonian (Dotzler et al., 2006). Also terrestrial fungi and fungi-like microorganisms have been reported from rocks as old as the Precambrian. The Early Devonian was representative by three fungal phyla: *Ascomycota, Glomeromycota and Chtridiomycota* (Krings et al., 2007). The role of AMF activity, along with a rich community of soil bacteria, must be addressed for a complete interpretation of the complex way bedrock is transformed under the impact of tree roots and soil biota.

Soil microorganisms are another key element of soils, both forest and agricultural. Microorganisms are an inseparable part of the soil environment and affect the functioning of ecosystems, plant health and soil structure and productivity (Nannipieri et al., 2003). The most important factors affecting the number and functioning of microorganisms include the availability of water and soil pH. Soils with a higher clay content, dominated by small pores sizes and higher pH, promote development of microorganisms, whereas less fertile, lighter and acidic soils are a better environment for the development of fungi. This phenomenon is one of the factors used to determine microbiological indicators for assessing soil fertility. The diversity and activity of microorganisms is determined by many biotic factors. However, the main factor limiting their development is the availability of organic matter. The composition of microorganisms can be an important determinant of the rate of decomposition of organic matter and circulation of nutrients and their availability in soils (Haack et al., 1995).

Some microorganisms can pioneer landscapes, forming initial soils, then as soon as plants enter the feedback begins - the plants interact with microorganisms and soils through the root secretions characteristic of each plant (Doran et al., 1996) and the contribution of decomposed organic matter to the soil matrix. The contribution of cyanobacteria to the development of Devonian plants is well described (Krings et al., 2007).

Microorganisms, creating multi-species communities, form a network of relationships between individual physiological groups, and affect plant health and productivity, soil structure and functioning of ecosystems. Synthesis and degradation processes carried out by communities of microorganisms should be seen as the sum of functions for which microbial communities are responsible, not just individual species (Garland and Millis, 1991). Studies on the activity of microorganisms in communities are necessary to learn about the ecology of microorganisms in biocenoses and should be analyzed in relation to existing environmental conditions. Knowledge of microbial functions and dynamics in natural environments is unfortunately limited, and analyzing biodiversity is not an easy task. To date, only a small percentage of prokaryotic microorganisms are described. It is believed that the soil environment is one of the richest reservoirs of microorganisms, since from 1 gram of soil can be isolated from 2,000 to 18,000 prokaryotic genomes. According to estimates of many microbiologists, only 0.1 to 10% of bacterial populations found in the environment are isolated on the basis of methods used today. Undoubtedly, soil microorganisms are a functionally very important group (Preston-Mafham et al., 2002).

5. Biomechanical weathering and its potential contribution to DPH

Biomechanical weathering is a type of biological weathering which integrates the effects of living organisms on physical changes in soils, regolith, and bedrock (Yatsu, 1988). This type of biological weathering was rarely studied and far greater attention was given to mechanical effects that could include biological factors, which historically included soil mixing, bioturbation, and biotransport (as defined by Johnson,

1993), for instance as a consequence of tree uprooting and root growth (Pawlik et al., 2016a, 2016b). Trees cause several biomechanical effects in soils, regolith, and bedrock, including (Phillips et al., 2017; Šamonil et al., 2018a):

1. hillslope surface disturbances, changes in roughness and heterogeneity mainly due to tree uprooting, tree root mounding, baumstaining, stemwashing, and tree breakage (Hoffman and Anderson, 2013; Pawlik et al., 2013, 2017, 2019; Šamonil et al., 2010a, 2015, 2017, 2018b);
2. exposure of fresh material to mass movements and water and wind erosion after soil is uplifted in the rootwad form (Pawlik, 2013), or due to rock fragment mining (Phillips et al., 2008);
3. driving of biogenic soil creep rates over longer time periods (Pawlik and Šamonil, 2018b; Šamonil et al., 2020);
4. soil production and soil accretion, factors which allow trees to be considered a land forming agent (Sullivan et al., 2016);
5. soil horizon simplification (soil homogenization) or differentiation (soil horizon heterogeneity) mainly due to pedoturbations (e.g., tree uprooting, soil mixing, soil horizon inversion; Schaetzl et al., 1989; Šamonil et al., 2010b, 2015, 2017; Daněk et al., 2016; Pawlik, 2013; Pawlik et al., 2016a, 2016b; Pawlik and Šamonil, 2018a) or biochemical effects of trees (e.g. decomposition of leaves, lying trunks with exposed root systems; Binkley and Giardina, 1998; Spears and Lajtha, 2004);
6. soil deepening (Phillips and Marion, 2006; Shouse and Phillips, 2016; Pawlik and Kasprzak, 2018) and rock cliff retreat (Jackson and Sheldon, 1949);
7. modification of biogeochemical cycles of elements in ecosystems (Lucas et al., 1993; Lucas, 2001; Perakis and Pett-Ridge, 2019; Houlton et al., 2018).

Compared to purely abiotic drivers of weathering, biomechanical weathering can potentially be much more effective due to a number of factors, e.g., roots extending into fractures to extract water (Akob and Küsel, 2011), but also water migration from trunk to roots and its surrounding in dry conditions. This is a hydrotropic response of roots and can be coupled with gravitropism. Both mechanisms lead to successful detection of fissures and crevices (Schenk, 2008; Poot et al., 2012). Root behavior provoked by hydrotropism and gravitropism is modified by negative root thigmotropism (growth away from an encountered object, Jaffe et al., 2002). This can be important from a biomechanical standpoint when a tree root grows in a narrow crack. Field measurements indicate that roots exert high pressure (> 7 kg/cm^2) at the growing root tips, in order to push their way through the soil (McNear Jr., 2013). In this context an important controlling factor of biomechanical weathering efficiency can be structural and is related to textural properties of bedrock and the way bedrock weathers under abiotic conditions.

6. Biochemical weathering and its potential contribution to DPH

Biological weathering is related to chemical weathering via the chemistry of living organisms (here, “biochemical” weathering). The rhizosphere is where bacteria, fungi and mycorrhizal fungi live in symbiosis and interact with tree roots. The rhizosphere is a narrow zone under the direct influence of roots and is rich in organic matter (OM), moisture, exudates, and organic acids, and supports a large quantity of microbes, greater than that found in non-rhizosphere soil (McNear Jr., 2013; Sokolova, 2011, 2015). The rhizosphere is also broadly defined as the volume of soil affected by the presence of roots of growing plants (Gregory, 2006). Rhizosphere volume in soils, sediments, or natural water can reach from 10^3 to 10^9 cells cm^{-3} (Banfield et al., 1999) or 10^9 microorganisms per gram of soil (Gałązka et al., 2012). Soil microorganisms play a major role in soil quality and functioning, largely determining soil structure and nutrient cycling, and ultimately impacting plant performance through nutrient mobilization, root growth, plant health. We propose that the influence of this living rhizosphere membrane over bedrock is not restricted to mature soils and can be significant on each stage of the soil production; from fractured weakly weathered bedrock to mature soil. One of the most important geochemical reactions mediated by biota in the rhizosphere is the transformation of biotite to vermiculite and kaolinite with the release of interlayer potassium (K) (Banfield et al., 1999). It was observed that uptake of K^+ by microbial cells and plant roots can lower the solution saturation state that indirectly promotes weathering. However, there are additional reactions and processes that take place in the rhizosphere which can directly or indirectly cause mineral weathering (R. Finlay et al., 2019a; R. D. Finlay et al., 2019b).

Microorganisms directly or indirectly cause mineral disaggregation, hydration, dissolution, and secondary mineral formation. They live mainly in the upper soil horizons but have also been found several kilometers below the Earth's surface (Pederson, 1993; Akob and Küsel, 2011). While some microorganisms live in solution, most are attached to mineral surfaces, resulting in dissolution, precipitation, and clay hydration reactions (Banfield et al., 1999). In soils, 80 to 90% of microbial cells exist in the adhesion state; that is, strongly attached to the surface of solid particles, where the most intensive weathering of minerals occurs (Sokolova, 2011). These microorganisms benefit from carbon-rich root exudates, and in response their living functions can accelerate weathering of minerals through excretion of 1) organic acids, 2) phenolic compounds, 3) protons, and 4) siderophores, i.e., compounds that chelate iron (Landeweert et al., 2001). Some authors argue that biochemical weathering is more important than physical weathering (Burford et al., 2003). In forest soils, microbes are most active within the rhizosphere and mycorrhizosphere, and mineral weathering is indeed more rapid than in a bulk soil without roots (Calvaruso et al., 2009; Uroz et al., 2009). Mycorrhizal fungi and bacteria (nitrifiers, thiobacilli, pseudomonades, and spore-forming bacteria) are the most active soil microbiota (Sokolova, 2011), and all have an active role in biochemical weathering.

In the mid-1990s, it was hypothesized that these microorganisms were responsible for tunneling of mineral grains through the hyphae of ectomycorrhizal fungi (Jongmans et al., 1997). This effect was documented mainly in Podzols (Sauer et al., 2007), and the fungi type was named rock-eating fungi (van Schöll et al., 2007). Tunneling of mineral grains is also seen in arbuscular mycorrhizal dominated forests (Koele et al., 2014). Mycorrhizal fungi can penetrate sites that cannot be reached even by the thinnest fine roots (non-vascular roots), such as intergranular mineral spaces. Phosphate weathering by mycorrhizal-liverwort symbioses can be 9-13 times stronger compared to plant-free situations (but owing to their shallow anchorage systems they were probably 10-fold less effective in impacting weathering flux than later-evolving trees in the early history of land plants; Quirk et al., 2015; Perakis and Pett-Ridge, 2019). Unfortunately, our ability to infer much beyond this discussion is limited because there is not yet substantial fossil-based information on fungal mycorrhizal symbionts in the rooting systems of the early trees (Strullu-Derrien et al., 2018).

7. Weathering magnitude due to plant evolution

Increased land surface weathering during the Ordovician-Devonian time has been taken into account by models such as GEOCARBSULF, COPSE and revised-COPSE, with differences between models in the overall strength of the effect of non-vascular and vascular (including trees) plants (Berner, 2006a; Lenton et al., 2018). The COPSE model assumes rapid plant evolution during 400-300 Ma and increase in weathering intensity. Revised-COPSE model assumes two-step interaction between weathering and plant invasion on land: 1) first stage of plant evolution at 450 Ma and related increase in weathering, 2) maximum level of weathering before 360 Ma linked to widespread evolution of forests. The two-step approach regulating weathering rates

Table 4
Examples of Devonian forest paleosols (Retallack, 1985, 1986, 1992, 2001; Mintz et al., 2010; Retallack and Huang, 2011).

USDA soil unit	Geological unit	Locality	Age	Tree species	Present analogue
Alfisols	Aztec Siltstone	Victoria Land, Antarctica	Givetian, 372 Ma	*Archaeopteris-Callixylon*	monsoon forest of sal (Shorea rubusta) in northern India
Inceptisol	Walton Formation (siltstone)	Near Hancock, New York, USA	Frasnian, 383-372 Ma	*Archaeopteris halliana*	-
Histosols	-	West Virginia, USA	Fammenian, 372-359 Ma	-	-
Arenosols	-	New York	Mid-Givetian (388-383 Ma)	*Callixylon*	dry riparian woodland
Ochrept, Fluvent, Vertisol and Inceptisol	Manorkill Formation	East Windham, NY	Middle Devonian (Givetian, 388-383 Ma)	*Wattieza, Archaeopteris*	fluvial levee (Ochrept), proximal to a fluvial channel (Fluvent), floodplain or fluvial terrace (Vertisol)

were also implemented in GEOCARBSULF model with first significant increase before 360 Ma and second at ca. 100 Ma related to the radiation of angiosperms 130-80 Ma (Berner, 2006a; Linkies et al., 2010; Lenton et al., 2018).

The whole family of GEOCARB models include diamensionless $f_E(t)$ parameter, the effect of plants on weathering rate (Berner, 2006b), and model outputs are sensitive to this parameter. Berner (2006b) highlights the large drop in CO_2 during the Permo-Carboniferous and attributes it to the rise of large vascular land plants, that accelerated the weathering of Ca and Mg silicates, and the burial of large volume of organic matter in sediments (Berner, 2006b). Similarly, Ibarra et al. (2019) model suggests that the strength of the silicate weathering feedback is driven by deep rooting vascular plants in the Late Devonian and Carboniferous.

Many studies support those modeling results, including enhanced weathering and nutrient flux through runoff and organic and inorganic carbon deposition, but a singular driving factor is frequently impossible to isolate experimentally or empirically. Percival et al. (2019) documented increase in osmium isotope ($Os_{(i)}$) composition of seawater values at the onset of the Kellwasser crisis at the FF boundary (Late Devonian) which they interpret in the light of enhanced continental weathering rates and subsequent marine anoxia leading to biotic crisis. This hypothesis, with some limitations highlighted by Percival et al. (2019), agrees with a documented detrital-influx and strontium-isotope ($^{87}Sr/^{86}Sr$) rise during the late Middle Devonian (Chen et al., 2005). The proxy data suggest enhanced weathering rates during the Kellwasser crisis. Even attribute this event to land plants activity, the long-term trend in $^{87}Sr/^{86}Sr$ values suggest continental weathering could also be attributed to climate warming and its positive effect on chemical weathering (van Geldern et al., 2006). It is still unclear whether land-plant evolution would have caused such pulses of high continental weathering during FF boundary. In this context two main negative arguments are commonly underlined: 1) short-lived nature of the FF biotic crisis is in contrast to long-term patterns of land plant evolution and soil production, and 2) a current lack of direct fossil evidence (Racki, 2005; Percival et al., 2019). Further, new data from D'Antonio et al. (2020) allows re-evaluation of the role of land plants in changes of weathering rates. Examining mass balance of the Earth's surface carbon cycle, they argue that the burial of terrestrial organic carbon commenced in the Devonian, as a result of CO_2 consumption and increase in terrestrial biomass, forced a reduction in silicate weathering rates, as compared to the pre-Devonian time. These results stand in contradiction to the main assumptions of DPH. However, this negative feedback could be also an outcome of climate cooling because the silicate weathering rate slows as the climate cools (Kasting, 2019).

8. Paleosols as indicators of biological weathering

One of the most important evidence of biogenic weathering processes, and an important place to address the knowledge gaps highlighted in the previous discussion, comes from paleosols, especially paleosols identified as forest soils. Retallack (1992a) emphasized that during the Paleozoic time diversification of soils was a product of the evolution of new kinds of vegetation, an assumption which is certainly true in terms of grass evolution and co-occurrence of Mollisols in Cretaceous (66 million years ago) (Retallack, 2001; Prasad et al., 2005). Driese and Mora (2001) conclude that during the post-Middle to Late Devonian large plants/trees were responsible for soil development mainly due to accelerated rates of weathering with positive feedback in thicker, better structured and horizonated soils. The argument of a direct response of pedologic system to vegetation change has been also used to support DPH (Algeo et al., 2001). Retallack (1992b) proposed classification of fossil soils on 'polsterland' and 'brakeland'. The first class constitutes well-drained soils dominated by lichens or plants lacking true roots. The second term describes well-drained soils dominated by herbaceous plants with rhizomes and roots not so densely turf-

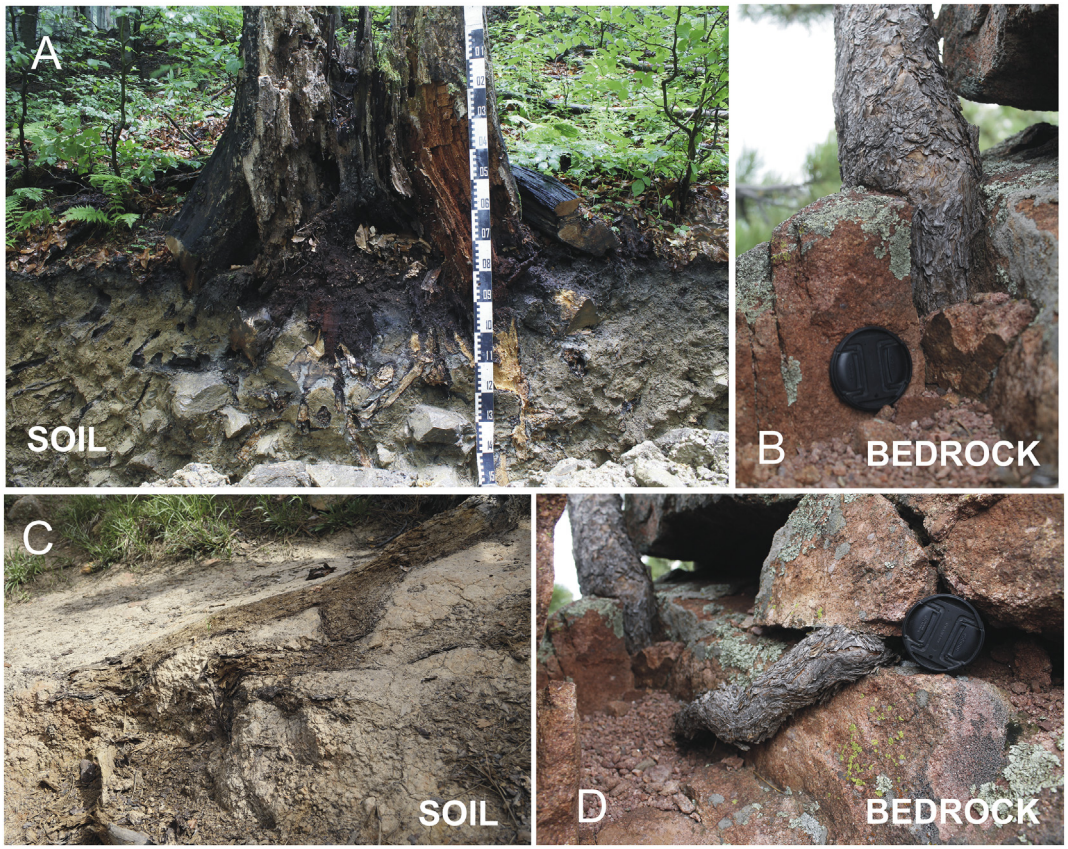

Fig. 7. Root architecture and potential root contribution to soil stabilization and bedrock mechanical weathering. A – European beech (*Fagus sylvatica*), Outer Western Carpathians, Poland; B, C, D – ponderosa pine (*Pinus ponderosa*), Colorado Front Range, USA. All photos: Ł. Pawlik.

forming as in grasslands. As bioindicators of early forest soils, Retallack (2001) mentions fossil stumps (see Mintz et al., 2010, for example), windthrows (probably seen as traces of treethrow pits), charcoal and associated cellular morphology, root traces, and also fossilized records of E (near paleosurface elluviation) and Bt and Bs (enriched, clayey or ferruginized paleosubsurface) horizons.

Probably the most ancient forest soils are Alfisols from Aztec Siltsone, Victoria Land, Antarctica, which bear traces of treethrow structures, large root traces, fossil wood, and spores of *Archaeopteris-Callixylon* (Table 4). The interpretation of Retallack (1997), though later criticized (Dahms et al., 1998), is in line with the current knowledge on Alfisols, i.e. 1) they are not initial soils, 2) they represent quite clear pedogenic process, which is clay illuviation, and 3) they contain clay minerals, usually resulted from alteration of primary minerals. Thus this soil might represent fossilized forest soil. Other soils, including Vertisols, became increasingly common during the Devonian whereas Ultisols and Spodosols originated in Carboniferous (Retallack, 1986; Algeo et al., 2001).

Paleosols are also a source of carbon isotopes (in carbonate nodules) and have been used as a proxy of atmospheric CO_2 in the past. Berner (2006b) compared these measurements with GEOCARB model outputs and concluded that both theoretical and empirical approach shows decrease in CO_2 during the Devonian.

9. Are Devonian trees the Biogeomorphic Ecosystem Engineers?

Finding evidence that plant evolutionary forces (namely occurrence of trees and forest ecosystems) were able to drive geomorphic evolution of landforms (through weathering, deterioration, accumulation and biotransport) would revolutionize our thinking on the importance of the evolution in geomorphology. Corenblit et al. (2009) and Steiger and Corenblit (2012) have already shown the potential of this concept and its application to river corridors, and steps have been made towards using biogeomorphology concepts to test theories about the origins of Martian landscapes (Corenblit et al., 2019). New landforms and river systems appeared along with gradual greening of the planet Earth through the Devonian (Gibling et al., 2014). Also, along with tree evolution and the widespread occurrence of deep root systems (e.g. *Archaeopteris*), a range of new processes and forms occurred and had impact on landforms and soil dynamics. This includes the tree uprooting process and pit-mound topography formation during which effective biotransport, soil mixing, and bedrock fragment mining occurs. Indirect effects related to trees, such as wildfires and subsequent soil erosion, also impact chemical composition of fresh and sea water (Gallaway et al., 2009; Kaiho et al., 2013). Tree uprooting may cause increase in sediment flux in river corridors over short- and long times scales. It also increases rates of biogenic creep (Pawlik and Šamonil, 2018b). Lu et al. (2019) found significant positive correlation between the proxies of terrestrial plant abundance (TAR – terrigenous-to-aquatic sources of organic mater, vitrinite and inertinite) and the proxies of continental input and weathering (SiO_2/Al_2O_3, CIA – chemical index of alteration and CPA – chemical proxy of alteration). Vitrinite and inertinite can be use as proxy because the first one is derived from wood tissue and the second from highly oxidized materials (charcoals). Earlier Marynowski (2007) presented evidence for occurrence of wildfires for the Upper Famennian.

Nowadays, trees are seen as contemporary ecosystem engineers, an important piece of landscape development and biogeochemical cycles (Gutiérrez and Jones, 2006). Through numerous biotic-abiotic and biotic-biotic feedbacks, trees also likely played a role in the evolution of other organisms (Brundrett, 2002; Occhipinti, 2013). Examples include oxygenation of atmosphere through photosynthesizing plants which is correlated with large predatory fish radiation in the Middle Paleozoic (Dahl et al., 2010) and giant insects evolution in the Late Paleozoic

Table 5
Global trends driving the Devonian landscapes. Authors' compilation based on references reviewed in this study.

Parameter	Trend	Causes
Plant cover	Increase	Evolutionary trends, positive trends in climate and land surface properties
Ecosystem complexity	Increase	Radiation of vascular and non-vascular plants and their symbiosis with microorganisms and fungi, adaptation to various land conditions
Biogeomorphic dominance	Increase	Increase in plant biomass, stature and rooting depth allowed to impact geomorphic processes
Atmospheric CO_2	Decrease	Various causes: consumed during photosynthesis and deposited as organic carbon, consumed during silicate weathering and precipitated as ocean bottom deposits
Atmospheric O_2	Increase	Positive feedback of plant evolution and photosynthesis
Temperature	Decrease	Due to negative impact in greenhouse effect
Volcanism	Increase	Siberian traps, lithosphere outgassing, marine anoxia
Fire intensity	Increase	Oxygen level over 17%
Soil erosion	Increase?	Due to increase in wildfires and decrease in soil stability
Weathering intensity	Increase	Due to positive feedback between plant, atmosphere and soil evolution, nutrient recycling, and microorganisms and symbiotic mycorrhizal fungi interactions with plants
Continental weathering rate	Increase?	Various isotopic indices and proxy data suggest this increase but the main driving factor or factors are still uncertain
Soil production	Increase	Various biotic and abiotic factors but is is frequently suggested that in terms of the Devonian soils deep-rooted vascular plants were the main cause. However, this process can be self-limited.

(Beerling, 2007; Harrison et al., 2010). However, ecological filtering can occur that negatively impacts particular taxa (Phillips, 2016a). In terms of trees this has been demonstrated by Binkley and Giardina (1998), who suggested that a tree species can modify soils to the disadvantage of other species. This is narrowly connected to the already tested ability of trees to deepen the soil horizon by repetitive occupation of the same site by trees of the same or other species (Phillips and Marion, 2004, 2006; Shouse and Phillips, 2016).

Physically, plants, especially trees with deep root systems, stabilize soil such that the effects of water and wind erosion are reduced (Fig. 7A and 7C). For example, in Central European mountain old-growth forests bioprotective function of trees represents at least 5 tons of soil and regolith per hectare (Šamonil et al., 2018b). This bioprotective role of trees might have had a fundamental impact on early soil evolution in the initial stage of plant expansion on land during the Devonian (Algeo and Scheckler, 1998). Following long-term stabilization of regolith and immature soils, plants were able to contribute to the physical and chemical weathering of bedrock, thereby contributing to further soil development. This is closely related to the possible effect described by D'Antonio et al. (2020) that plants could increase the silicate weathering feedback strength, but not silicate weathering rates. Hence, there is a clear positive feedback between the stabilizing function of trees and rock/mineral weathering by tree roots, although at fine-scales some hillslopes (e.g., high wind exposed locations) could be dominated by tree uprooting process (Phillips et al., 2017). This issue, together with several other topics including weathering, soil production, and climate change, has been discussed in many papers on DPH (Algeo and Scheckler, 1998; Algeo et al., 1995, 2001).

Chemical effects are also likely. For example, trees can drive carbonate rock dissolution in karst regions (Phillips, 2016a). However, investigation of this question in Devonian landscapes is still in its initial stage and needs further consideration. Small-scale root structures such as root grooves or karren also suggest an important role of tree roots in bedrock alteration by chemical weathering (Zseni, 2009). As shown by Jakucs (1977) these structures develop under compact soil where roots etch into the limestone surface or penetrate along joints. Further, the author explains that formation of these subsoil corrosion channels is accelerated by the root acids of plants and intense CO_2 production of microorganisms surrounding the root system (Zseni, 2009).

It is still not known how rapidly tree roots can break up rock (Fig. 7B and 7D). There is also a question of causality, which asks what developed first: an existing rock fissure, or a tree root that promoted the development of the fissure (Yatsu, 1988). We believe there needs to be an initial fissure which can then be penetrated by fine roots. Similar hypothesis proposed Brantley and Eissenstat (2017) who assumed that "*tree roots can only physically penetrate and biogeochemically comminute the immobile substrate underlying mobile soil when that underlying substrate is fractured or preweathered*" (p. 5117). Under enhanced chemical weathering conditions, a root is able to grow and finally be replaced by large roots (with vascular tissue). Along with root growth, gradual enlargement of a crack takes place. However, this was only partly proved (Malik et al., 2019). Recently some biologists suggested that plants maximize their chance of encountering fractures by spreading their roots along the rock surface, but also that detection of crevices in the rock could be a result of gravitropism, hydrotropism, or a combination of both (Schenk, 2008).

In the light of extensive evidence on the present role of trees and forest ecosystems, we conclude that trees are able to change hillslope and river dynamics, influencing biotransport, bioweathering, and pedoturbations. They also influence climate properties and hydrological cycle. Though further research is undoubtedly required, we argue that trees are effective biogeomorphic ecosystem engineers currently. However, we find only two pieces of evidence (supported by geological evidence) to allow similar conclusion regarding Devonian trees (or tree-like plants): 1) co-evolution with river systems from braided to meandering, and 2) co-evolution with new soil types. It seems that in these two cases, BEE by trees is clear and increased in strength through the Devonian and Carboniferous as a results of biogeomorphic succession (Table 5). In other cases of geomorphic changes plant fossil record is still too incomplete and largely dominated by wet lowland palaeoenvironments. Thus the scale and scope of effect remains unknown. Global events, both supported by models and proxy data, are frequently seen in the light of land plant radiation, occurring because of the first arborescence vascular plants and forest ecosystems (Table 5). However, the wide range of possible explanations and triggering factors must be taken into account. Isolation of any specific role of trees seems to be impossible now. There is widely accepted view that forest ecosystems impacted Devonian climate (via changes in albedo, precipitation, surface roughness, CO_2 consumption and oxygen production) and hydrological cycle (via interception and transpiration, inhibition of soil erosion) (Table 5). However, it is still unclear whether trees were able to migrate to uplands (far from open water sources) and positively affect weathering and soil production processes. Definite prove of this tree expansion and functions via fossils would greatly support still widely explored Devonian Plant Hypotheses.

10. Knowledge gaps, future work and perspectives

Both DPH and the role of BEE in the Devonian needs further research. The following problems need urgent attention of the scientific community:

1. the relationship and functions of non-plant organisms in rooting zone of Devonian trees, based on existing and new fossil evidence.

The status, structure, and function of mycorrhizal associations with the Devonian trees is important but uncertain.
2. ecophysiology of the Devonian plant species
3. detail plant anatomy description and information about phenotype which would help in biogeomorphic interpretations
4. evaluation of the Devonian ecosystems (structure, density, etc.) and their disturbance regime based on new and complete fossil evidence (not only individual plants)
5. better understanding of current and past biomechanical weathering and soil production induced by tree roots via new molecular, microbiological, and geochemical methods
6. further geochemical evidence and isotopic proxy data from land and marine deposits that would help to test DPH
7. evaluation of existing data in the light of co-evolution of trees and soils in the Devonian
8. stronger understanding of the spatial distribution of trees and forests in the Devonian, not just limited to streams and lowland environments.

Acknowledgments

Jan Sovák is thanked for preparation and permission to use the image of the Devonian landscape. Mariusz Salamon is thanked for his comments on the earlier draft of the manuscript. Christopher Scotese generously shared his data on the Devonian palaeogeography. Paul Kenrick is thanked for the discussion on the main topic of this paper, and Jan Golonka is thanked for sharing his publications. This study was supported by the Polish National Science Centre (OPUS 17, project no 2019/33/B/ST10/01009). Attendance of Pavel Šamonil was supported by the Czech Science Foundation, project no. 19-09427S. We thank Professor Thomas J. Algeo and an anonymous reviewer for their constructive comments and suggestions that allowed to improved the final version of our manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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